

## STUDIES ON AUSTRALIAN THYNNIDAE (HYMENOPTERA). II.

## A SHORT HISTORY OF THYNNID TAXONOMY.

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*Synopsis.*

An account is given of investigations leading to the recognition of the generic characters, geographical distribution, and association of the very dissimilar sexes, as well as an account of the promotion of the Fabrician genus *Thynnus* to the family category Thynnidae. Male wasps became known to science as *Thynnus* and females as *Tiphia* in 1775. Subsequently, as collections came from Australia many new species were described and new genera were erected. These genera were later grouped together into a single genus *Thynnus* by Klug, whose ideas strongly influenced Smith, and later Dalla Torre (1897). Not till early in this century was the genus *Thynnus* reclassified into a number of genera, firstly by Ashmead (1903) and later by R. E. Turner. This author published a major revision with the first key to species in 1907-8 and a generic revision in 1910. He described many new species. It has now been suggested by Pate (1947) that the reduction of Thynnidae and some half dozen related families to the rank of subfamilies of the family Tiphidae would better illustrate their phylogenetic relationships.

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INTRODUCTION.

The history of Thynnid taxonomy forms part of a project which, when completed, will be a monographic revision of the family. It is the second paper of this series and follows in sequence with the catalogue read to this Society on 25th November, 1953. Revisions bring their changes, and it is anticipated that some modifications of former classifications will be suggested. A brief account is presented here of the contributions on the Thynnidae made by earlier naturalists, which are now our heritage. The works of these contributors are reviewed in chronological order, and the influence exerted by one author over others is most evident. There is a great deal to be learnt from an examination of the achievements of these pioneers, and it is most interesting to trace the account of the discoveries they made of the various features which are of fundamental significance in this study.

The object of the present paper is to review the work of some forty naturalists published between 1775 and 1947, as taxonomic revisions are founded on the achievements of earlier workers. It is the second step in this revision and tells of the accumulation of our knowledge of Thynnidae over a period of one hundred and thirty-eight years. The present paper is an acknowledgement of the achievements of former workers, as the information they have compiled on the numerous known species makes it possible to carry out further investigation in this field.

## SUMMARY.

Fabricius introduced flower-wasps to Science when he described them from the Joseph Banks collection. The male specimens he called *Thynnus dentatus*, *Thynnus emarginatus*, and *Thynnus integer*, while certain apterous, ant-like individuals in the collection he named *Tiphia pedestris*, unaware that they were the females of his new genus *Thynnus*. Since Fabricius, many naturalists have contributed towards our

knowledge of this interesting group. A suitable taxonomic character that would separate *Thynnus* from other wasps was recognized in thynnid wing-venation by Jurine (1807). Klug's description of *Scotaena trifasciata* showed that thynnid wasps occurred in South America as well as in Australia and, as their absence was noted from collections made in other countries, the geographical isolation of these insects in South America and Australia was established.

As a result of the voyage of the *Coquille*, the number of species of thynnid known was increasing, and to Guérin-Méneville, these forms differed sufficiently from *Thynnus* to be described as separate genera. Soon afterwards, Klug (1840) published a monograph in which all of Guérin's genera were discarded and his species united into one single genus, *Thynnus*. Like most Linnaean and Fabrician genera, *Thynnus* became elevated to family rank. It was first disassociated from its allies and classified as a separate family by Shuckard (1840) and (1841). Guérin (1842) opposed the conception held by Klug of the use of the generic category, and erected further genera. Additional species were described by Westwood (1844), and in later years many more were added to the family by Frederick Smith and by Saussure (1868). Froggatt (1891) and Dalla Torre (1897) catalogued Thynnidae, but while Froggatt retained many existing genera, Dalla Torre listed all species alphabetically into one single genus, *Thynnus*. Taxonomic categories have a different value in different periods of taxonomy and Ashmead (1903) gave a classification of Thynnidae into a series of new genera. Dominating all else in this history is the contribution made to our knowledge of the Thynnidae by Rowland Edward Turner, a British hymenopterist who travelled extensively and made an enormous collection of these insects. In particular we are indebted to him for his revision of the Thynnidae (1907) and (1908), with its many new species. We are also indebted to Rowland Turner for his important generic revision, *Genera Insectorum* (1910), and for the many descriptions of new species that were contributed by him during the years that followed. Montet (1922) described more new species of the Thynnidae. The use of the most appropriate taxonomic category was again reviewed by Pate (1947), who contended that in the interests of phylogeny the family Thynnidae should be demoted in favour of subfamily Thynninae, family Tiphidae. This brief history of the study of thynnid taxonomy begins with Cook's first voyage and terminates with Pate's suggested grouping of the thynnids as a subfamily of the family Tiphidae.

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The author wishes to express his sincere appreciation of certain most helpful conversations with Mr. Anthony Musgrave, of the Australian Museum, on the subject of entomological history. It is largely due to the interest so aroused that the present paper was attempted. His bibliography and history of Australian entomology have been of great assistance in this study.

#### HISTORICAL REVIEW OF LITERATURE ON THYNNIDAE.

*Johann Christian Fabricius, Johann Roemer, and Christ.*

The history begins in 1770 when Captain James Cook in H.M. Barque "Endeavour" sailed homeward along the shores of northern Queensland and made collections at various landings on the coast. The type locality is presumed to be Endeavour River, now Cooktown, since Cook was delayed there for seven weeks between 18th June and 5th August, or possibly Bustard Head on 24th May, or Thirsty Sound on 30th May, 1770 (Wharton, 1893). Three species of male wasp and one species of female were collected and the original specimens have been preserved to this day in the Joseph Banks Collection in the British Museum.

The insect collections from New Holland were sent to Johann Christian Fabricius (1745-1810) of Denmark for description. Our flower-wasps were first described in his *Systema Entomologiae* (1775). The males were named *Thynnus dentatus*, *Thynnus emarginatus* and *Thynnus integer*, and as the dissimilarity between the sexes is so very great the female became known as *Tiphia pedestris*.

Our present-day Order Hymenoptera had already been established by Linnaeus (1707-1778), who had selected the general form of the wings in insects as a means of separating one group from another. Linnaeus had already defined our Orders Hymenoptera, Coleoptera, Hemiptera, Lepidoptera and Neuroptera in the tenth edition of his *Systema Naturae* (1758). On the other hand, Fabricius had been investigating the mouth-parts of many of his genera of insects, and set out to create a classification based on the comparative morphology of mouth-parts. In his *Systema* (1775) Fabricius grouped in his Order Synistata the *Ephemera*, *Lepisma*, *Podura*, *Hemerobius*, *Myrmeleon* and all Hymenopterous genera including *Thynnus*. Difficult though it is to believe, this group even included *Oniscus*. An abridged version of the *Systema* (1775) followed, called the *Species Insectorum* (1781). This was a reprinting word for word of the initial, abbreviated statement that he gave in his former work to define his genus and species. Six years later the *Mantissa Insectorum* (1787) was produced and here for the third time his original, cryptic definition was printed and his Order Synistata remained unchanged.

Roemer (1789) magnificently illustrated many of the genera that had been described by both Linnaeus and Fabricius, and a beautiful (hand coloured) illustration exists of *Thynnus dentatus*, accompanied by the classic Fabrician extract. This was followed by the thirteenth edition of the *Systema Naturae* which was revised and enlarged by Gmelin (1790), twenty-two years after the death of Carl von Linné. Gmelin retained the Linnean Order Hymenoptera rather than the Fabrician Synistata, and supplied a little more information on the structure of their mouth-parts.

Christ (1791) in *Naturg. d. Insect.* considered that the genus *Thynnus* should be sunk as a synonym for *Vespa*, that *Tiphia pedestris* should become *Sphex pedestris*, and that *integer* should become *integra*.

For eighteen years Fabricius retained his *Thynnus*, *Tiphia*, and all the hymenopterous genera in this heterogenous order Synistata, until eventually he modified this extraordinary classification in his *Entomologia Systematica emendata et aucta* (1793). With mouth-parts still his taxonomic characters, he separated the genera which comprise our Hymenoptera from his Order Synistata and placed them in a group by themselves, the *Piezata*. The descriptions of 1775 were duplicated in full, with one additional contribution, *Thynnus abdominalis*, from Africa, a species which subsequently was shown to be a bee. Three years later came the *Index Alphabeticus Entomologiam Systematicam emendatam et auctam* (1796), which gave the page references to the preceding Fabrician volume. Then Fabricius (1804) produced his *Systema Piezatorum*, embodying eighty-three hymenopterous genera classified on their antennae and mouth-parts. Coloured illustrations of *Thynnus dentatus*, *Thynnus emarginatus*, *Thynnus integer* were given by Donovan (1805).

*Pierre Andre Latreille and Louis Jurine.*

Thirty years after the generic name *Thynnus* had been proposed by Fabricius, Latreille, who was at that time working at the Paris Museum, published his *Histoire Naturelle des Crustacés et des Insectes* (1805). During that thirty-year period flower-wasps had been mentioned in ten separate publications, but the only additional information contributed were the illustrations of Roemer (1789) and of Donovan (1805). In fact, monotony characterized the recurring Fabrician contributions of those early, static years. Several interesting comments were made on *Thynnus* by Latreille (1805), which were based on information supplied to him by the Rev. W. Kirby, of England. "Cette division générique de Fabricius est composée de quatre espèces qui sont presque d'autant de genres différens. 1° Le thynne denté, figuré par Roemer, peut être pris pour le type du genre; la 2° espèce paroît être encore un thynne; la 3° est une mégachile, et la 4° est probablement une myzine. Le savant entomologiste anglais Kirby a eu la complaisance de me donner des éclaircissemens très-bien détaillés sur ces thynnes de Fabricius, qui ont été décrits dans la collection de Banks." It is evident that Latreille's concepts of the generic category differed considerably from those held by Fabricius, and other examples in this history show the truth of the following statement: "A genus

or other category has a different value in different historic periods of taxonomy" (Mayr *et al.*, 1953).

Jurine (1807) described the genus *Thynnus* in his *Nouvelle Méthode de Classer les Hyménoptères et les Diptères*. He characterizes the genus as having "Cellule radiale, une, étroite, très-allongée. Cellules cubitales, quatre, presque égales et carrées: la 2<sup>e</sup> et la 3<sup>e</sup> reçoivent les deux nervures recurrentes; la 4<sup>e</sup> atteint le bout de l'aile."

Latreille (1809) in his *Genera Crustaceorum et Insectorum* gave a new description of *Thynnus*, and a new genus for *Tiphia pedestris*. For *Thynnus* he even attempted to discriminate between the males and what he thought, *in error*, to be the females! As for *Tiphia pedestris*, he was no longer satisfied that this ant-like insect was in any way related to the genus *Tiphia*, and he therefore removed *T. pedestris* to a new genus, *Myrmecodes*, which he had erected for it. Latreille considered that *Thynnus* should belong to the family Scolietae together with *Scolia*, *Sapygia*, *Myzine*, *Tengyre*, and others. On the other hand, *Tiphia pedestris* was grouped in the family Mutillariae, and so Latreille divided the males into male and female sexes, and succeeded in classifying the males (*Thynnus*) and the true females (*Myrmecodes*) into separate families. His reference to wing-venation reads: "Areola marginalis anastomosi obsoletissima" and "Alae superae areola marginali soluta seu costae immediate non adjecta; areola submarginali prima anastomosi distincta secata."

*Klug, Olivier and Lamarck.*

By 1810 the first thynnid wasp from South America had arrived in Berlin, and it was described by Dr. Klug as *Scotaena trifasciata*. The existence of Thynnids in the unique faunas of both South America and New Holland was thus established, and as collecting continued in other countries, it was found that thynnids did not occur elsewhere. About the same time another interesting event occurred. This was the discovery of a second female thynnid. Olivier (1811) associated it with Latreille's *Myzine* (1804) and it became *Myzine aptera*. This drew attention to Latreille's recent new genus, *Myrmecodes*. Only a half-dozen thynnids were known in 1811. There were four males, *Thynnus dentatus*, *T. emarginatus*, *T. integer*, and *Scotaena trifasciata*, and two females, *Tiphia (Myrmecodes) pedestris* and *Myzine (Myrmecodes) aptera*. Lamarck (1744-1829) gives a short account of *Thynnus* in his *Annales sans Vertèbres* (1817) and presents, almost word for word, a well-edited version of the ill-conceived notions set forth by Latreille (1809) regarding the differentiation of the sexes. Although *Myrmecodes* had been shown to be the female of *Thynnus* some time before the second edition (1835) appeared, his editors omitted to rectify this error. Lamarck's version of Latreille (1809) on sex differences reads: "Antennes filiformes, presque sétacées, plus courtes et plus épaisses dans les femelles que dans les mâles. Mandibules étroites, saillantes, arquées, subunidentées plus fortes dans les femelles. Les yeux des femelles entiers. Corps allongé, presque linéaire dans les mâles."

*Leach and Kirby.*

In 1818, forty-three years after Fabricius had named them, there was still only a little information recorded on *Thynnus*. There were some specimens from New Holland which were collected by Robert Brown, who had come here as the botanist on the Matthew Flinders Expedition, which set out from England in the *Investigator* in 1801. This expedition is linked in our history with the adoption of the name "Australia" for our continent. Its use had been advocated by Flinders as early as 1804 rather than either New Holland or New South Wales, and in his *Voyage to Terra Australis* (1814) preference for the name was expressed by this explorer (Australian Encyclopaedia, 1925). Robert Brown left Port Jackson in 1805, and the thynnids in his collection were described by Kirby (1818) and by Leach (1819). Kirby gave us *Thynnus variabilis*, adopting his name from Leach's manuscript, and also *Thynnus annulatus*. Leach followed this with a variant of *T. annulatus* which he named after Brown; however, *brownii* has become a synonym for *T. annulatus*. In the same year Latreille (1818) produced his celebrated *Nouveau Dictionnaire d'histoire naturelle*, which refers both to *Thynnus* and to *Myrmecodes*.

*Lepeletier de Saint-Fargeau.*

The work of Lepeletier (1825) is a reproduction of Latreille and the idea that the winged form was bisexual is retained. He also gives Jurine's description of wing-venation. In his second paper (1845) his error regarding sex differentiation is omitted, and his description of wing-venation reads: "*Caractères des ailes.* Une radiale ovale, grande. Quatre cubitales; la première séparée en deux par une nervure descendant de la côte sans atteindre le cubitus. La seconde reçoit la première nervure récurrente. La troisième cubitale reçoit la deuxième récurrente. La quatrième, assez courte, atteint le bout de l'aile."

*Van der Linden, Friedrich Klug, Boisduval, John Westwood and William Shuckard.*

Interesting contributions regarding the discovery that *Thynnus* and *Myrmecodes* were in fact male and female forms of the same insect group were made. Van der Linden (1829), with Wesmael, showed that a European species related to *Thynnus*, *Methoca ichneumonoides* (♀) (Famille des Mutillaires), was the female form of *Tengyra sanvitali* Latreille (1809) (♂) (Famille des Scolietes). A little later Klug (1831), in discussing the eyes of insects, writes: "In den Gattungen *Mutilla* und *Apterogyna* haben die Männchen deutliche, die ungeflügelten Weibchen dagegen keine Ocellen. Ebenso verhält es sich mit den Gattungen *Myrmosa*, ferner *Tengyra*, zu welcher *Methoca* und *Thynnus*, zu welcher die Gattung *Myrmecoda* als Weibchen gehört" (p. 307). Then Boisduval (1835) gave his short description in the *Voyage de l'Astrolabe* of *Thynnus australis*, Port Weston, but unfortunately his type was lost, so his species has never been finally determined from his illustrations, or his few colour characters. This was followed by Westwood (1835), who defined *Diamma bicolor*, female, in a few well-chosen words. By strange coincidence the next species described was the male of *Diamma bicolor* Shuckard (1836), which the author named *Psamatha chalybea*, stating: "It may subsequently prove to be the male of Westwood's *Diamma*." Shuckard had guessed from analogy that *Myrmecodes* was the female of *Thynnus*, and this supposition was confirmed by a Mr. Lewis, of Sydney, N.S.W., who observed *Thynnus variabilis* in copula with an apterous female congeneric with *Tiphia* (*Myrmecodes*) *pedestris*.

*Guérin-Méneville.*

An event which could be called a "milestone" in this history was the contribution made by Guérin-Méneville (1838) in the Duperrey's memoirs of the *Voyage Autour du Monde* by the corvette *La Coquille* (1822-1825), which had visited both New Holland and South America. This voyage was by Royal Command, and therefore the account of its achievements was published on an appropriately lavish scale. Guérin's Atlas (1832) illustrated *Thynnus* (?) *rubripes* (♂), and also *Myzine australis* (♂) (later *Anthobosca australis*), showing mouth-parts and hypopygium; it bears the date (Novemb. 15th, 1831). Guérin's contribution on the thynnids in the Duperrey memoirs was a monograph. Hymenopterous genera allied to *Thynnus* and the wingless nature of their females were discussed and an important advance was made in the classification of the wasps belonging to this group. The thynnids were placed in the *Mutillaires*, which were "Hyménoptères vivant solitairement et n'offrant que des mâles ailés et des femelles aptères", etc. The scheme followed was simple:

Famille des *Heterogynes*:

Tribu: I. *Formicaires*: Ants.

Tribu: II. *Mutillaires*: Eighteen genera, including *Thynnus*.

Famille des *Fouisseure*:

Tribu: I. *Scolietes*: *Scolie*, *Tiphie* & others.

Tribu: II. *Sapygites*: *Sapyge* & others.

A key is given to the eighteen genera of the *Mutillaires*. All his new species were described in every detail with complete disregard for printing costs. Former descriptions of the earlier species were reprinted, some with additional information. Eleven new species and the genera *Rhagigaster*, *Agriomyia*, *Thynnoides* and *Tachypterus* were described from Australia.

*William Shuckard and Ferdinand Erichson.*

Shuckard (1840) was the first to elevate *Thynnus* Fabricius (1775) to the taxonomic category family *Thynnidae*. Of preceding authors, Latreille (1809, 1819) associated *Thynnus* with famille *Scolietae*; Kirby (1819), Sphegidae; Latreille (1818) and Lepeletier (1825), famille des Fousseuse, tribu des Sapygites; while Westwood (1835), Shuckard (1836), and Guérin (1838) grouped them with Mutillidae. When more material was examined (presumably), the separation of the Thynnids from Mutillids would naturally follow, as these insects are quite dissimilar. The extent of Shuckard's acquaintance with this group is illustrated by this abstract from *On the History and Natural Arrangement of Insects* (1840): "Apterogyna: *Thynnus* has apterous females, numerous cognate genera and many species. The legitimate partners of several of them are known. The latter were ascertained from observations of friends in New Holland, where except for several genera, the whole family is found. It is into this family that *Elis* F. enters. The females of the *Thynnidae* show remarkable structures." Shuckard's index reads: "Thynnidae, structure of p. 176." In the following year a new genus and species was described by Shuckard (1841) in *Grey's Journal of Two Expeditions*; this was *Oncorhinus xanthospilosus*. This description is under the heading "Hymenoptera (Family Thynnidae Shuckard)", and in the introduction he writes: "My reasons for establishing the Family Thynnidae, I shall expose in my monograph of that family, which would have been published ere this but for the difficulty in procuring specimens for dissection . . ."

In those days there was an annual report compiled by Erichson, in which an account was given of the current entomological publications. Prior to 1841, thynnid publications were listed with Mutillidae. In Erichson (1843), *Bericht über die Wissenschaftlichen Leistungen im Gebiete der Entomologie während des Jahres 1841*, in which *Oncorhinus xanthospilus* Shuckard appears, Erichson follows Shuckard's lead and classifies his information for that year and for all subsequent years under the title *Family Thynnidae*. Erichson (1842), *Beitrag zur Fauna von Vanämensland*, etc., described four new species of *Thynnus* and erected the new genus *Ariphron*, using the female. These new genera and species were duly noted by Erichson in his next *Bericht* for the year 1842, published in 1844, but no description of the characters of the family Thynnidae as such were set out in Erichson's works. Although Erichson had definitely established Shuckard's priority as the original author of the taxonomic category *Family Thynnidae* by publishing his report of Shuckard's *Oncorhinus* paper of 1841 in the *Bericht* for that year, and by reporting his own *Ariphron* paper of 1842 in the subsequent *Bericht* for the year 1842, Louis Agassiz in the *Nomenclator Zoologicus* credits as its author: "Family Thynnidae Erichson, in Weigmann Arch. 1842." This blatant error has been duplicated by Thynnid workers to the present day.

Shuckard's promised monograph on the family Thynnidae, in which his taxonomic characters were to be presented, unfortunately never appeared. In its stead, Klug (1840) produced his monumental work on *Über die Insectenfamilie Heterogyna Lat. und die Gattung Thynnus F. insbesondere*. It was clear that these two authors held opposing views as regards splitting and grouping of genera, and it is regretted that Shuckard's work was lost. Presumably this author's manuscript was abandoned with the entry of both Klug (1840) and Guérin (1838) into the field.

*Dr. Klug.*

Klug, who was a doctor of medicine in Berlin, wrote a most impressive monograph on these insects, which he classified as *Insectenfamilie Heterogyna* Latreille, *Gattung Thynnus*, Fabricius. It would be impossible to deal both adequately and briefly with his work. Klug retained the older concept of the genus, as held by Linnaeus and Fabricius, and refused to accept the modern outlook of Guérin-Méneville, and consequently grouped all the genera erected by Guérin and others into one single, all-embracing genus, *Thynnus*. However, he erected a new genus, *Aelurus*, from Brazil. He divided the genus *Thynnus* into four *Unterabtheilung*, and the method he employed will be discussed by the present author in a subsequent paper. It is safe to say that

the subsequent workers in this field were strongly influenced regarding the usage of the taxonomic category *genus*, by the Linnaean concept held by this medical practitioner.

*Guérin-Méneville.*

After Klug (1840), Guérin-Méneville (1842), one of the leading entomologists of that period, produced his final paper on the Australian Thynnidae, *Matériaux sur les Thynnides*, which is illustrated by some very excellent figures. In his opening lines he begins: "Depuis la publication de notre travail dans le *Voyage* de Duperrey nous avons augmenté notre collection de Thynnides, . . . Déjà M. Klug, dans sa monographie du genre *Thynnus*, a fait connaître quelques unes des espèces sur lesquelles nous avons fait des études sérieuses, et il est probable que les observations qui nous restent seront perdues, si nous attendons que M. Shuckard ait donné la monographie des Thynnides, qu'il prépare."

Guérin considered that many species were sufficiently distinct to justify their classification into separate genera. In his latest contribution Guérin added three more new genera and twelve new species to the ever-growing list of Thynnidae, showing his thorough disregard for Hrn. Friedrich Klug and his monograph! Although Klug had sunk every single genus of the Thynnidae that had been erected by Guérin, and had amalgamated them all into *Thynnus*, the concept of the generic category held by this celebrated author remained unchanged. The specific names selected perpetuate the names of his contemporaries—Shuckard, Westwood, Spinolae and Klug, in fact with a twist of humour, Guérin attaches Klug's name to a new species belonging to yet another of his new genera. In Guérin's second group of Australian genera were *Tachynomyia*, *Catocheilus* and *Lophocheilus*.

*John Westwood.*

In three papers, Westwood (1844) presented a summary of the more important parts of Guérin's outstanding contributions, made appropriate comments on Klug (1840), summed up the taxonomic characters of ten species of *Rhagigaster*, gave us additional information on *Diamma* (1835) and other species, and made very full descriptions of twenty-one species of Thynnideous insects. No entomologist at that time set so fine an example, no one but Westwood could more appropriately deliver the following simple exhortation to his fellow workers: "The recent monographs of Dr. Klug and Guérin-Méneville . . . and the different results at which these distinguished hymenopterologists have arrived respecting the generic arrangement of these insects, render the observation of every fact, tending to determine the question at issue, absolutely necessary." Despite Westwood's careful work and his call for explicit descriptions, the second half of the century was characterized by ambiguity and brevity in most of the descriptive work written on the Thynnidae. Klug's influence prevailed and in the subsequent decades the only genus to be erected was *Zeleboria* Saussure.

*Frederick Smith.*

In complete contrast to the peak in this history attained in the early forties by such competent workers as Shuckard, Guérin, Klug and Westwood, the latter part of the nineteenth century gave rise only to numbers of meagre descriptions of new species. The principal figures in this era were Frederick Smith and Henri de Saussure; while of lesser consequence were Ritsema (1876), Olliff (1889), and David Sharp (1900). The catalogues of Froggatt (1891) and Dalla Torre (1897) brought the period to a close.

Outstanding amongst his contemporaries for the numbers of new species of Thynnidae he described was Mr. Frederick Smith, hymenopterist in the British Museum, who from 1859 to 1879 described one hundred and sixty-nine Australian and twelve South American species of Thynnidae. In 1859 Smith published his catalogue of the Hymenoptera in the British Museum and, according to this volume, the Thynnidae comprised two hundred and nineteen species. Of these, forty-eight came from South America and one hundred and seventy-one species came from Australia. That the family was limited to these two geographically isolated continents was now well established. It is of interest to notice that Frederick Smith's work was published in the same year as Darwin's "Origin" and also that Smith's name is mentioned by

Darwin in connection with *Formica sanguinea*, a slave-making ant. Not only was Smith acknowledged in "The Origin of Species", but by coincidence the family Thynnidae became associated also with the work of Alfred Russel Wallace, as it was Frederick Smith (1859-65) who made a catalogue of the Hymenoptera collected by A. R. Wallace, which included a dozen Thynnidae from such places as Aru, Batchian, Ceram, Gilolo, Mysol, Waigiou, Bouru, Salwatty, Morty and New Guinea. So these extensive collections made in the East by A. R. Wallace showed that the Thynnidae range into Austro-Malaya.

Many of Smith's earlier descriptions were based on superficial features alone. In fact, colour pattern was the chief feature that Smith attempted to describe, with brief reference to pubescence and surface puncturing. In consequence, many of the descriptions in the Catalogue of 1859 are hopelessly inadequate, and their identification, from literature that deals with so many species so very briefly, would be completely impossible. Of the array of species described by this author there are some that have had to be sunk as synonyms of his own species, for Smith was apparently prepared to make a new species out of any of the various colour variants that he could find. It is not without interest to notice the effects upon Frederick Smith of the two conflicting schools of thought which immediately preceded him. Klug's impressive monograph had re-established the genus *Thynnus* as conceived by Fabricius. Consequently the line of least resistance would be to name new Thynnidae as species of the genus *Thynnus*. This course was far easier for Smith than the erection of new genera, and the subsequent discrimination of generic characters; thus many complications were fortunately avoided. Klug's new genus *Aelurus* was now in vogue, and the fact that Klug's two species were South American did not deter Smith from following Westwood's lead and cataloguing *Agriomyia* (*Tachynomyia*) *abdominalis* Guérin (1842) as the first example of an *Aelurus* from Australia. Guérin's other genera, *Thynnoides*, *Agriomyia*, *Lophocheilus* and *Catocheilus*, were regarded by Smith, as they were by Westwood, as being merely of subgeneric value. Likewise, *Enteles* Westwood and *Eirone* Westwood were grouped with *Thynnus*. The genera which Smith retained were: *Rhagigaster* Guérin (1838), *Oncorhinus* Shuckard (1841), *Ariphron* Erichson (1842), *Diamma* Westwood (1835), *Tachypterus* Guérin (1838), *Iswara* Westwood (1851), and *Anthobosca* Guérin (1838). He accepted Louis Agassiz (1842-6) regarding authorship of Thynnidae even with publication by Shuckard (1841) beside him. *Iswara* and *Anthobosca* do not belong to the Thynnidae.

#### *Henri de Saussure.*

In 1868, concurrent with Frederick Smith in England, Henri de Saussure published his descriptions of Hymenoptera collected on the voyage of the *Fregatte Novara*. This included twenty-four species of the family Thynnidae. By Saussure the family was regarded as *Tribus Thynnii*, which was divided into two *Legio*:

Legio 1<sup>a</sup> (♂) Prima areola cubitalis apice haud divisa.

Prima vena transverso-cubitalis integerrima.

Mandibulae tridentatae. (♀) incognitae.

Legio 2<sup>a</sup> (♂) Prima areola cubitalis apice per ramum venae transverso-cubitalis divisa (vel appendiculata).

Venae recurrentes sigillatim a 2<sup>a</sup> et 3<sup>a</sup> areola cubitali exceptae.

Mandibulae bidentatae. (♀) Thorax transverse tripartitus.

In the first legion were *Tachypterus* Guérin and *Oncorhinus* Shuckard, which were separated on the relationship between the *vena recurrentes* and the *areola cubitalis*; it also included *Anthobosca*, which is not Thynnidae. In the second legion were *Elaphroptera* Guérin, *Rhagigaster* Guérin, *Thynnus* Fabricius, *Tachynomyia* Guérin, *Iswara* Westwood, *Elaphroptera* Guérin, *Zelevatoria* Saussure, *Aelurus* Klug. Separation of these genera was achieved by means of the form of the hypopygium, first cubital cell, the segments of the maxillary palp, and the shape of the abdomen. The subgenera *Agriomyia* Guérin and *Thynnoides* Guérin were retained, together with the subdivision of *Thynnus* proposed by Klug (1840). Recognition was also made of the genera *Eirone* Westwood (1844), *Enteles* Westwood (1844), *Diamma* Westwood (1835), and *Ariphron*



Erichson (1842). This author holds the distinction of being the only systematist to erect a new genus in the fifty-nine years that elapsed from 1844 to 1903. This is the genus *Zebeboria* Saussure (1868). *Z. carinata* is Saussure's type; it also includes *Thynnus xanthorrhæi* Smith (see further Turner, 1910, and Rohwer, 1910).

*C. Ritsema, Arthur Olliff, Walter Froggatt, William Kirby and David Sharp.*

Ritsema, Olliff, Froggatt, Kirby and Sharp contributed towards our knowledge of the Thynnidae. *Aelurus flavopictus* Ritsema (1876), n. sp., first recorded from Aru Island, but later known from North Queensland and New Guinea; a common mainland species, *T. campanularis* Sm. was found to roam as far as Lord Howe Island, Olliff (1899); Froggatt (1891) records *T. pulchralis*, *T. brenchleyi* from Narrabri, N.S.W., and *Rhagigaster integer* from Victoria Desert, S.A. *Thynnus taeniolatus* Froggatt (1893), n. sp., was described from the Elder Expedition. Kirby (1898) mentions three species discovered at Palm Creek and Illamurta by the Horn Expedition to Central Australia, and briefly describes *Rhagigaster illustris*. Lastly, Sharp (1899), in *Cambridge Natural History*, writes a short note on these insects, using *Methoca ichneumonoides* as an example.

*Walter Froggatt.*

An important contribution to our knowledge of the Thynnidae was made by Walter Froggatt (1891) in his catalogue of the described Hymenoptera of Australia, in which there were twenty pages listing the species of this family. The ten genera which had been retained by the preceding authors are given by Froggatt, and the number of described species amounted at that time to two hundred and fifty-one. He writes: ". . . there is, no doubt, a good deal of confusion in this family, and a revision of the Thynnidae would be very useful work." This catalogue gives the author, date, sex, and locality of the described species, but as the complications of synonymy had never been investigated, the work is primarily a register of specific names. In the genus *Thynnus*, one hundred and ninety-two species had been described by 1891, among which, included as subgenera, were Guérin's *Agriomyia*, *Lophocheilus*, *Catocheilus* and *Thynnoides*, together with Westwood's *Eirone*. The type species of *Aelurus* Klug came from Brazil, but it is interesting to notice that Smith (1859) had catalogued *Tachynomyia abdominalis* Guérin, the type species for *Tachynomyia*, into Klug's genus *Aelurus*, and that this genus now contained some seventeen Australian species, many of which had been described by Smith. *Tachynomyia*, cut off from its type species, only contained the two species that Saussure had described. *Rhagigaster* Guérin had twenty-six species, *Zebeboria* Saussure had four species while *Anthobosca* Guérin, later to become family Anthoboscidae, contained five species. The three, historically important, monotypic species, *Diamma bicolor* Westwood (1835) (♀), *Oncorhinus xanthospilus* Shuckard (1841) (♂), and *Ariphron bicolor* Erichson (1842) (♀), were all retained, while a synonym for the male of *Diamma*, *Tachypterus fasciatus*, was also listed. This was *T. crassicornis* Smith, which has subsequently been removed to the Anthoboscidae.

*Dalla Torre.*

The nineteenth century closed with the publication of the *Catalogue of Hymenoptera* by Dalla Torre (1897). It was fortunate that Froggatt had completed and published his list of our native species before the appearance of Dalla Torre's work, in case, like Shuckard's monograph, Froggatt's catalogue had also to be abandoned. These two catalogues provide interesting comparisons, as Froggatt listed, without alteration, the genera and species described, while Dalla Torre introduced certain taxonomic changes in his contribution. With several exceptions this author united all the genera of Thynnidae into one single genus, *Thynnus*. The exceptions were *Tachypterus*, which Dalla Torre combined with *Diamma* and *Psamatha*, and *Iswara* from India, which belongs to family Myzinidae. By thus grouping together *Aelurus*, *Ariphron*, *Anthobosca*, *Zebeboria*, *Tachynomyia*, *Rhagigaster* and *Oncorhinus* into one genus, *Thynnus*, a number of species which shared the same specific names became automatically congeneric and duplication of various names resulted once their former genera had lapsed.

Dalla Torre therefore proposed new names, but unfortunately certain errors resulted. However, fourteen of these have subsequently been rectified by Schulz (1906). The Dalla Torre catalogue is an alphabetical inventory of world Thynnidae, in effect of the genus *Thynnus*, and contains three hundred and thirty-seven species, with valuable references. The influence of Klug's monograph, followed by the addition of Smith's numerous species to *Thynnus*, resulted in the inclusion within this genus of a very great diversity of forms. The work of various authors was inconsistent and, as a study of comparative morphology had never been made, the taxonomy of Thynnidae was now highly confused.

*William H. Ashmead.*

Ashmead (1903) considered that the Myrmosidae, the Mutillidae, and the Thynnidae were three separate families of the superfamily Vespoidea. In his opinion, the family Thynnidae should be divided into three distinct subfamilies, the Thynninae, the Rhagigasterinae, and the Methocinae. According to this author, the subfamilies Thynninae and Rhagigasterinae comprised thirty-seven genera from Australia and South America and also an Indian genus, *Iswara*. There are no Methocids in Australia.

Ashmead constructed keys to the subfamilies and genera of the family Thynnidae, using the morphology of the hypopygium, thorax, mandibles and wing-venation as his taxonomic characters. His publication appeared in 1903; following soon after the Dalla Torre catalogue, it shows an important advance in the history of Thynnid taxonomy. Here, after sixty years, was a complete reversal of Klug's concept, and this was the first constructive attempt towards a generic classification of the group since 1838, when Guérin gave his simple keys to the thynnid wasps found on the voyage of *La Coquille*. In seventy-five years construction of keys to this group had become a complex problem. When Guérin worked on the Thynnidae there were only thirty-eight species recognized from South America and Australia, but by 1903 the number of described species had increased to three hundred and forty. Furthermore, much of Smith's work was so superficial that it could have been of little assistance to Ashmead. Although it is evident that Ashmead made a study of these insects and was acquainted with their morphology, the use of his generic key would be quite impracticable. Insufficient was known of the Thynnidae at that time, and this work seems to have gone to press prematurely. Ashmead at least presented a notable attempt, which was made more difficult for him by the excessive number of species and the total inadequacy of the preceding literature. Considered in relation to the period when his study was made, Ashmead presented a positive approach to the problem of a classification of the family into subsidiary taxonomic categories. His was the only comparative study of these wasps since the days of Guérin and Westwood, and it stands in marked contrast with Frederick Smith's descriptions and the index presented by Dalla Torre.

Ashmead's generic keys contain anomalies which are difficult to comprehend. For instance, this author erected a new genus *Aeolothynnus*, using as its type the name of a manuscript species *Aeolothynnus multiguttatus* Ashmead, and omitted to publish his description or define this species in any way. In Ashmead's key to the male Thynninae, taxonomic characters of *Myrmecodes* Latreille (type species, *Tiphia pedestris* Fabricius) are set out, but the male of this classical species has never yet been recognized. It is difficult to understand how Ashmead could have placed conspecific species into separate genera. For instance, *Agriomyia abdominalis* and *Agriomyia spinolata* are conspecific, but Ashmead identified one of these as Guérin's original type species for *Tachynomyia*, and used the other as the type for his new genus *Pseudaelurus*. *Agriomyia maculata* Guérin and *Thynnus (Agriomyia) odyneroides* Westwood, which are also synonymous, were classified respectively as Guérin's type species for *Agriomyia* and Ashmead's type species for his new genus, *Cephalothynnus*. Two genera which do not belong to the Thynnidae, *Anthobosca* and *Iswara*, appear in this generic key.

*Gunther Enderlein, Peter Cameron, and W. A. Schulz.*

Enderlein (1904) described his new genus, *Homalothynnus*, which has subsequently been discarded. *Thynnus albopilosellus* Cameron (1906) was described from expeditions

into Dutch New Guinea. Schulz (1906) corrected certain errors in the Dalla Torre catalogue, and followed this (1908) with descriptions of *Enteles wagneri* and *E. sanguineiventris*, n. sp.

Rowland Edward Turner.

This field of research has since been dominated by Rowland Edward Turner, who worked voluntarily for the British Museum of Natural History for thirty years on various Hymenoptera and became a recognized authority on the Thynnidae. Turner's *Revision of the Thynnidae of Australia*, Part i, 1907; Part ii, 1908, contained the first key to the species, with synonymy, redescriptions of earlier species, and many additional descriptions of new species. This was followed in 1910 by Turner's key and catalogue to world Thynnidae. Here the family is divided into three subfamilies, the Diamminae, the Rhagigasterinae and the Thynninae. Turner recognized forty-seven genera, of which thirty-four are Australian, and in his catalogue he lists three hundred and fifty-six species from this country. Thynnid taxonomy was completely changed by the advent of this new classification.

Rowland Turner, Allen Rohwer, G. Montet, Joseph Bequaert and Delfa Guiglia.

There have been one hundred and thirty-three new species described, one genus erected, and adjustments made to four generic names since 1910. Thus the combined total number of species would amount to 489 but for the fact that a number are synonyms; the number recognized by Turner appears to be 475. Of the above authors, Turner described one hundred and fifteen new species and a new genus in his series of fifteen papers. Fourteen species were contributed by Montet (1922), Rohwer gave us three, while a single species was added by Rayment. Rohwer's paper of 1910 is important, as it clears several errors made by Turner in his generic names. Bequaert (1926) established the date of Guérin in Duperrey as 1838, and Guiglia (1948) described the condition of Guérin-Ménéville's types preserved in the Museo di Genova.

V. S. L. Pate.

Pate (1947), in his *A Conspectus of the Tiphidae* states: "The Tiphid wasps have for the most part been treated as a collection of separate and distinct families: the Bradynobaenidae, Myrmosidae, Anthoboscidae, Tiphidae, Myzinidae, Thynnidae and Methocidae . . . it is not difficult to show that a division which accords many, if not each, of these groups separate family status gives no adequate picture of the phylogeny of the group. Indeed there is much to say in favour of including all these wasps in the single family Tiphidae, which may then be divided into a number of subfamilies corresponding to as many phylogenetic strains." In the thynnids the values placed on taxonomic categories have varied at different times in this history. So also has the application of these categories by various authors in general zoology, and the assignment of the rank of superfamily, family, or subfamily is subjective. According to Mayr, Linsley and Usinger (1953): "A family may be defined as a systematic category including one genus or a group of genera of common origin, which is separated from other families by a decided gap." Further investigation will be required before the extent of such a "gap" can be assessed. However, should these seven groups prove to be sufficiently dissimilar one from another and by Mayr's definition conform to family rank, then in conformity with established taxonomic procedure, it would be more appropriate to use the categories Superfamily and Family in place of Family and Subfamily, provided that no inconsistencies arise between existing superfamilies and such a new superfamily as Tiphioidea.

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